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VARIATION IN SECTION TRIGONOPHYLLAE OF NICOTIANA

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Section *Trigonophyllae* of the genus *Nicotiana* is peculiar to the warm deserts of southwestern North America, and ranges from California to Texas and southward locally as far as Oaxaca. The section, as defined by Goodspeed (1954), includes two species: *N. trigonophylla* Dunal, the range of which coincides with that of the section, and *N. Palmeri* Gray, which is apparently found only in southwestern Utah and western Arizona.

During the course of an ecological investigation of *N. trigonophylla* throughout its range in the United States, the writer encountered facts which cast doubt on the validity of the specific rank of the taxon *N. Palmeri*.

The two members of the section *Trigonophyllae* are segregated as follows by Goodspeed (1954) in his key and text:

Calyx 8-11 mm. long; corolla 12-23 mm. long, limb 3-4 mm. wide, erect in bud; seed ca. 0.5 mm. long; cauline leaves obtuse to acuminate....*N. trigonophylla*

Calyx 15-17 mm. long; corolla 23-32 mm. long, limb 5-6 mm. wide, oblique in bud; seed ca. 0.7 mm. long; cauline leaves acute to acuminate.....*N. Palmeri*

Both taxa have the same chromosome number (12 pairs) and Kostoff (1943) reported that F₁ hybrids between the two show twelve homologous pairs of chromosomes at meiosis.

The writer visited several of the major herbaria¹ of the United States and examined the collections of *Nicotiana*, section *Trigonophyllae*. Only

nine collection numbers were encountered which were labelled or annotated as *N. Palmeri*. Of these, one was an intermediate mentioned by Goodspeed (1954), and of the remaining eight specimens only two possessed corollas appreciable larger than those of *N. trigonophylla*: 1) *Keck 4255* (UC) Gillespie Dam, Maricopa County, Arizona, March 22, 1936. "In lava rock at cliff base." 2) *Gould 1611* (NY) St. George, Washington County, Utah, April 20, 1942. "Southern slope of Black Hill . . . on rock ledges and among volcanic boulders." Both of these specimens have corollas more than 30 mm. in length. This is larger than the type collection (*Palmer 433*), which is intermediate between these extremes and *N. trigonophylla*.

In the herbarium at Dixie College at St. George, Utah, there were seven collections of section *Trigonophyllae* from the basalt-capped mesa just west of St. George (the site of *Gould 1611*). Of these, only one was labelled *N. Palmeri*; the other six (including one determined by I. Tidestrom) were labelled *N. trigonophylla*. None were more than intermediate between the two taxa. On the other hand, the writer has grown plants from seed collected from this same site which produced corollas 27 mm. in length, which is within the size range for the flowers of *N. Palmeri*.

Specimens and seed were collected over a large part of the range of section *Trigonophyllae* in the United States. Measurements of various taxonomic characters were made both on collected plants and on plants grown from seed in the greenhouse. The results are presented in Table 1, where a number of size classes are established for each character investigated. The number of measurements falling within each size class is given, thus illustrating the modal class and the range of variation. For the greenhouse-grown plants each figure represents the number of plants having that particular mean character size, while for the collected specimens, each figure indicates the number of measurements falling in a size class.

The populations investigated show a trend toward *N. Palmeri* characters as one approaches the Washington County, Utah area. Whether one regards *N. Palmeri* as a distinct species or prefers to sink it to the subspecific or varietal level, it is apparent that the two taxa are not clearly delineated, but intergrade with respect to all characters measured. This morphological intergradation is probably best interpreted in a topoclinal sense, since no ecological gradients appear to be involved. In the range of *N. Palmeri*, section *Trigonophyllae* occupies its three usual ecological niches: 1) bedrock outcrops and talus; 2) dry washes; 3) ruderal sites (roadsides, etc.), but it is most prevalent in the first mentioned (Wells, 1959).

¹ The following institutions were visited: Bureau of Plant Industry (Beltsville, Md., Missouri Botanical Garden, St. Louis, New York Botanical Garden, Rancho Santa Ana Botanical Garden, Claremont, California, University of California, Berkeley, and the United States National Herbarium, Washington, D.C.

The tendency of plants of section *Trigonophyllae* to occur in small, isolated populations, and the localization of plants showing *N. Palmeri* characters in certain northwestern portions of the range of the section, suggest the operation of the Sewall Wright effect in bringing about differentiation. A related possibility is the selection of larger flowers by some local pollinator in the *N. Palmeri* range.

The taxon *N. trigonophylla* Dun. is acknowledged by Goodspeed (1954) to be a variable one. With respect to the validity of *N. Palmeri*, Goodspeed (1945) wrote: "... *N. Palmeri* is morphologically so closely related to *N. trigonophylla* as doubtfully to deserve specific recognition ...". In his 1954 monograph, he wrote: "This species (*N. Palmeri*) is obviously close to *N. trigonophylla*. It is distinguishable even from large flowered races of the latter by the greater coarseness throughout, by longer corolla, and by broader, whiter, more horizontal limb with lobes at times slightly concave. *Maguire and Blood 1456*, 15 miles SW of Leeds (Washington Co.), Utah (UC) is an example of an intermediate between the two."

In the herbarium of the New York Botanical Garden, there is a series of collections of section *Trigonophyllae* from Sonora and Baja California. On one of the herbarium sheets (*MacDougal 41*), there are some remarks by a reviewer of these collections (unsigned). In summary, he finds the material "not uniform but contains 2 forms with very different pubescence. One is densely glandular villous-tomentose and is so oily as to heavily stain collecting paper. The two forms deserve nomenclatural recognition, but at present it seems impossible to determine which is typical form. *N. Palmeri* Gray of Arizona seems intermediate in its characters, but nearest to eglandulose form." The writer also found wide variation in several characters (including flower size) in the Mexican collections of section *Trigonophyllae*. It seems likely that an intensive study of the *N. trigonophylla* complex in Mexico might uncover variants at least as divergent as the currently accepted *N. Palmeri*.

Considering the variability of *N. trigonophylla* and the continuous intergradation between it and *N. Palmeri*, and also the very meager representation of the latter taxon in herbaria, it does not seem too conservative to relegate *N. Palmeri* to subspecific or varietal status. This, in fact, has already been done by Marcus E. Jones (1908) who reduced *N. Palmeri* Gray to *N. trigonophylla* Dun. var. *Palmeri* (Gray) Jones.

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